

DYNAMICS OF VEGETATIVE SHOOTS OF THREE SPECIES OF *AFRAMOMUM* (ZINGIBERACEÆ) IN CAMEROON

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ABSTRACT : Demography of leafy shoots was monitored for a year in 3 *Aframomum* species, rhizomatous herbs. Emergence rate of new shoots showed four oscillations in one species but a single maximum in two species. Growth rates were highest while the shoots were leafless, and declined steadily with increasing height. Herbivory by primates may increase emergence and growth rates. All species showed mortality precisely related to shoot age, with maximum shoot longevity in the range of 1.2-1.5 years. Diverse relationships of phenology to climate, and of vegetative to sexual phenology, were shown in these species and two other herbs of the same habitat.

RÉSUMÉ : Une étude de population de rameaux feuillés a été faite pendant 1 an sur 3 espèces d'*Aframomum* (herbes rhizomateuses). Dans une de ces espèces, la répartition annuelle du taux d'apparition de nouveaux rameaux montre quatre sommets, mais n'en montre qu'un seul chez les 2 autres. Les taux de croissance sont les plus forts tandis que les rameaux sont encore aphyllés, puis décroissent régulièrement avec leur accroissement en hauteur. Les taux de croissance et d'apparition des rameaux semblent accrus par leur consommation par des Primates herbivores. Chez toutes ces espèces, la mortalité est en relation précise avec l'âge du rameau, la longévité maximum d'un rameau étant de l'ordre de 1,2-1,5 an. Chez ces espèces, et chez les 2 autres herbes partageant leur habitat, on montre diverses relations entre la phénologie et le climat, et entre la phénologie végétative et sexuelle.

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Appearance, growth and death among the many units of a branched plant are the focus of the demographic perspective on clonal growth (HARPER, 1978). The dynamics of some rhizomatous plants has been studied in temperate habitats, but tropical counterparts have been illucidated only from the architectural perspective (BELL, 1979; HALLÉ, 1979). Here I report actuarial data on giant herbs of disturbed areas in equatorial forest. In this setting important considerations include the strong seasonality of rainfall, and herbivory by large mammals. Observations are presented on turnover and growth rates within the standing crop of leaf-supporting shoots, comparing three congeneric species at one site: *Aframomum giganteum* K. Schum., *A. hanburyi* K. Schum., and *A. subsericeum* K. Schum. (Zingiberaceæ).

GROWTH HABIT

Each sympodial unit of an *Aframomum* clone begins as a subterranean lateral branch on another shoot. Each branch has a rhizomatous stage

of horizontal growth, but for most branches this lasts only a few internodes, and these internodes are quite short. The branch then turns upward, beginning the upright growth that is of concern here. On the shoot, leafless sheaths to a height of about 1 m are followed by a close array of distichous leaves. A 6 m shoot of *A. giganteum* may bear 43 leaves, and a 3 m shoot of *A. subsericeum* may bear 30 leaves. These shoots are strictly vegetative, and of indeterminate growth though each species and grove has a fairly well-defined maximum height, in the range of 2-6 m. Death of the entire shoot may be rapid, or very slow with death of the leaves in descending sequence.

Groves of some species are apparently structured by a bimodal tendency in the length of the rhizome stage; e.g. in *A. daniellii* "rameaux tracants et non-tracants" respectively have 11-15 and up to 70+ internodes (HALLÉ, 1979). *A. giganteum* and *A. hanburyi* groves both have superficially uniform canopies but the stems arise in clumps. In one grove of *A. giganteum* the highest variance in numbers of stems per plot occurred at the smallest plot size, 0.0625 m², indicating that stems "clump" most strongly at that or a smaller scale. New clumps would be initiated by the stems with a prolonged rhizome stage (number and/or length of internodes). Other tactics of spatial disposition of shoots are known, *A. polyanthum* lacking long branches, and *A. aff. sulcatum* lacking short branches (HALLÉ, 1979).

Leafless flowering branches arise from the rhizomes, distal to vegetative branches (HALLÉ, 1979). The species differ in the structure and size of the inflorescence. Pollination may be by sunbirds, and several mammals, including four primate species, disperse the seeds.

SITE

The study area was near the southern border of the United Republic of Cameroon, Campo subdistrict, in the vicinity of Nkoelon village (2° 23' N, 10° 3' E; ca. 200 m elev.). Four seasons were defined by rainfall, there being a 3-4 week drought about July, and a 3 months drought from December through February (Table 1). However, the number of rainless days per 28-day period exceeded 14 days in 10 of 13 consecutive periods, and 12 % of the year's rain fell in a single week in October. The soil of the area is a ferralitic latosol, which supports "Biafran Forest", a floristic unit described by LETOUZEY (1968). Logging disturbance, 2-6 years previous, amounted to 8.4 % of the area (BULLOCK, 1980), of which about half was suitable for development of *Aframomum* groves.

SAMPLING

The three species studied were the most abundant of perhaps 10 species of *Aframomum* occurring in the region, and were among the most common of all herbs along roadsides and in old fields. The species can be found

scattered through the forest, but differences in success in various microhabitats are as yet poorly defined.

The three species were studied for 8-12 months from July 1976-June 1977. Observations were made every four weeks on fixed plots. For simplicity, dates are reported here by day numbers; thus day 001, 1 January 1977, was near the midpoint of the study. The new shoots found and given identification numbers each month are referred to below as the emergence cohort for that month. (No seedlings appeared in the plots). The emergence rate is the number of these new shoots divided by the number of shoots living at the previous census. A mean emergence date for each cohort is taken as two weeks prior to the first observation of the cohort. The height of each shoot was recorded each month, and refers to the distance from the center of a basal bulge of the stem to the ligule of the uppermost, green, expanded leaf, or to the tip of the spike for shoots consisting only of bladeless sheaths. The heights reported here are mean heights for cohorts or designated portions of cohorts: this includes the means at ages of two and six weeks, and a "standard maximum height". The latter represents, for *A. giganteum*, the maximum height of the tallest half of the early emergence cohorts; for *A. hanburyi*, it is the height of the tallest half of the initial (mixed-age) cohort present on the plots. Mortality is considered for the entire population of each grove (new deaths divided by the number of live shoots in the previous census), for age classes of shoots independent of emergence date, and for the initial populations of the plots.

Numbers of flowers and fruits in different stages were also noted. Comparative notes on the phenology of other common herbs are presented in the Discussion.

All the plots were associated with logging disturbances.

There were two plots of *A. giganteum*. Ag1 was 8 × 8 m with an initial density of 2.4 shoots/m², on level ground, with bulldozer-mounded earth behind the plot, and no tree cover. This grove was advancing into a stand of the shrub *Stachytarpheta*; dead shrubs and dead standing shoots of *A. giganteum* were removed from the grove in early July 1976, and some additional shoots were cut in late July, late August and mid-September. Ag2 was 5 × 9 m with an initial density of 3.0 shoots/m², on bulldozer-mounded earth, with no tree cover.

Three plots of *A. hanburyi* were observed. Ah1 was 5 × 3 m with an initial density of 5.2 shoots/m², aligned along the edge of an old dirt road, with encroaching branches of *Harungana madagascariensis* and *Macaranga sp.*, and morning shade from taller trees of *Musanga cecropioides*. Ah2 was 5 × 2 m with an initial density of 6.0 shoots/m², situated on an old tractor trail, and one end of the plot was seasonally water-logged; the high tree canopy was half-closed. Ah3 was 5 × 2 m with an initial density of 4.7 shoots/m², situated on an old tractor trail, with partial shade from saplings and a high, broken tree canopy.

A single grove of *A. subsericeum* was observed, beginning in December 1976, on a 3 × 4 m plot with an initial density of 7.1 shoots/m², on level ground, with a light canopy of *Harungana*.

RESULTS

Aframomum giganteum

In Ag1, the highest emergence rate (.91 new shoots/old shoot/month) followed initial clearing of standing dead shoots and dead shrubs from the grove (Table 1). High emergence also followed the next cuttings, but the rate of mid-October (.29) probably reflected the rainfall maximum as well. The rate then declined and was lowest through the major dry season (.01-.04), increasing again through May and June (.11, day 178). In Ag2,

TABLE 1 : EMERGENCE, GROWTH AND MORTALITY RATES

Emergence and mortality are for entire groves on given census days; growth (cm increment in mean height) applies to the emergence cohort of the given day; (* Ah1 only). Rainfall totals (mm) are given for the four weeks preceding each census.

	CENSUS DAY													n=
	207	232	256	291	315	347	010	038	066	094	122	150	178	
<i>Ag1</i>														
Emergence	.91	.27	.10	.29	.08	.04	.01	.04	.01	.03	.05	.08	.11	505
Growth 0-2 wks	54	42	33	68	44	129	86	59	102	58	63	46	49	503
2-6 wks	93	72	136	106	120	110	89	88	98	159	166	129	—	449
Death		.05	.08	.02	.04	.09	.12	.10	.07	.08	.07	.09	.10	215
<i>Ag2</i>														
Emergence		.11	.06	.22	.29	.09	.07	.03	.03	.06	.03	.05	.04	234
Growth 0-2 wks		74	92	106	94	88	92	45	46	71	75	107	108	191
2-6 wks		129	165	139	135	152	114	138	114	134	133	115	—	174
Death		0	0	0	.04	0	0	.04	.02	.04	.04	.04	.03	39
<i>Ah</i>														
Emergence		.14*	.04	.13	.11	.06	.05	.07	.11	.04	.10	.10	.09	188
Growth* 0-2 wks		51	45	143	120	114	84	103	86	50	58	92	98	113
2-6 wks		92	168	79	85	123	125	124	137	152	114	113	—	99
Death		.05	.09	.08	.07	.12	.04	.12	.06	.07	.07	.14	.16	201
<i>As</i>														
Emergence							.04	.07	.04	.05	.09	.06	.07	34
Growth 0-2 wks							48	53	19	34	40	45	34	34
2-6 wks							63	64	78	73	40	64	—	25
Death							.08	.06	.11	.04	.05	.07	.11	40
RAINFALL	20	28	93	270	420	89	4	46	110	85	136	194	12	

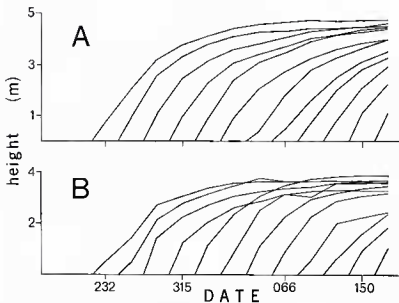


Fig. 1. — Mean height of shoots for each emergence cohort throughout the study period; each line traces the history of a particular emergence cohort. (A) is Ag2, (B) is Ah1; only four of the twelve census dates are specified.

exact emergence rates could not be calculated as only shoots new during the study were marked and monitored, so mortality among the pre-existing shoots isn't known. Nonetheless, the highest emergence rate was clearly in the wettest month (ca. .29, Table 1). The rate declined through the first half of the major dry season, not reaching a minimum until the February census. Between February and late June there was no trend in emergence rate.

The greatest increments in shoot height were during the first six weeks (Fig. 1, A; Table 1). The mean height of shoots at the first observation of any cohort ranged from 33 to 129 cm. The overall means among cohorts for the first two weeks were 64 ± 27 cm for Ag1 and 83 ± 22 cm for Ag2. The variation in this height did not reflect current rainfall, nor did the two groves show parallel variation. In Ag1, relatively slow growth was typical (55 ± 14 cm, 11 cohorts) compared to other cohorts there (116 cm, 2 cohorts), and to both slow and fast-growing shoots in Ag2 (94 ± 13 cm, 7 cohorts and 142 ± 20 cm, 5 cohorts). The mean growth increment for the following month ranged from 72 to 165 cm for both groves (Table 1), with averages of 114 ± 29 cm for Ag1 and 133 ± 16 cm for Ag2. This increment showed some tendency to be higher in cohorts emerging in wetter months. The monthly increment declined steadily for four or more months (Fig. 1), becoming somewhat irregular after that, though close to

zero. The standard maximum heights were 463 ± 63 cm for Ag1 ($n = 70$) and 501 ± 22 cm for Ag2 ($n = 25$).

Excluding the October and November censuses, the mean natural death rate in Ag1 over the year was .085/month (Table 1). There was a marked minimum at the height of the wet season (.02-.04), and somewhat higher than average values were recorded in January and February (.12 and .10). In addition, there was mortality from cutting of .09 in August and .05 in September. The exact rates could not be calculated for Ag2, as with emergence, but the crude number of deaths among marked shoots showed no trend from February through June.

The age-specific mortality in Ag1 was constant, as reflected by the linear survivorship curve (Fig. 2, A), with a loss of .05 per month ($r^2 = .99$, $s_b = .002$). The regression predicts a half life of $10\frac{1}{2}$ months and that all the shoots would be dead before the 21st month. Ag2 had high initial survivorship, .987 for 0-8 months ($r^2 = .97$, $s_b = .001$), but there was a dramatic change to a rate of .907 for ages 9-13 months ($r^2 = .97$, $s_b = .002$; Fig. 2, A). If the latter rate remained constant, the last shoots would have died before 19 months age.

Aframomum hanburyi

Emergence rate in *A. hanburyi* averaged $.084 \pm .03$ between the three groves over the whole study period. However, more or less regular fluctuations occurred in the emergence rate; the timing in the three groves was slightly different but the mean behavior was representative (Table 1). Peak emergence ($>.10$) was in October-November, March, and May. These observations extend over only 44 weeks, and the longer record for Ah1 suggested that a fourth peak occurred in August.

The greatest increments in shoot height occurred in the first two months (Fig. 1, B; Table 1). At the first observation of cohorts in Ah1, mean shoot height ranged from 45-143 cm. The minimum values occurred at the August, September, early April and early May censuses, and these averaged 51 ± 5 cm, less than half the average of the other months (105 ± 20 cm). The mean increment in the next month ranged from 79-168 cm, with an average among cohorts of 119 ± 27 cm, but the lowest values were for the two cohorts with the greatest initial growth. The trend in growth for subsequent months was similar to that for *A. giganteum* (Fig. 1, B). The standard maximum height was 315 ± 50 cm ($n = 38$).

There was also a substantial change in height distribution over the year for Ah1. Whereas only 23 % of the initial population was taller than 300 cm, at the final census 58 % surpassed this height. The difference was apparently due to a decrease in herbivory by arboreal primates (probably *Cercopithecus nictitans*): 19 % of the shoots present initially were obviously eaten or broken distally, but only 6 % were so damaged at the final census.

Peak mortality was in May and June, with secondary peaks noted at

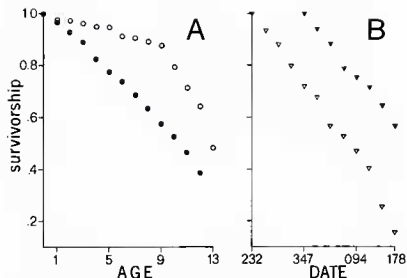


Fig. 2. — Survivorship (A) as a function of age (months) in *A. giganteum* (● is Ag1, ○ is Ag2), and (B) as a function of time in the initial mixed-age population of *A. hanburyi* (▼) and *A. subsericeum* (▲).

day 348 (due to Ah2) and at day 039 (due to Ah1). The average mortality in the other months was $.07 \pm .02$ (Table 1).

Age-specific mortality for *A. hanburyi* was higher in the first three months than in the following eight, so the survivorship curve was slightly concave. However, the sample was less than 50 shoots for all ages over six months, and at several ages no mortality occurred in this small sample. Extrapolation of the mortality of the first four months in Ah1 (.044) predicted 23 months would elapse before the death of all shoots of one emergence cohort. About 74 % of all deaths (in both Ah1 and Ah2) were concentrated in the initial mixed-age cohorts. The initial cohort in the two groves (combined $n = 134$) showed a loss of .07 per month (Fig. 2, B; $r^2 = .99$, $s_b = .004$), and the regression predicted the entire cohort would have died by the 14th month.

Aframomum subsericeum

In the one plot of *A. subsericeum*, emergence rate averaged $.06 \pm .02$ for the seven months for which data are available (censures of day 011 through day 179, Table 1). The mean height of shoots at the first observations of each cohort ranged from 19-53 cm. The lowest value was recorded in early March, and the average among the other months was 42 ± 8 cm. In the following month the increment ranged from 40-78 cm, with a mean of 64 ± 13 cm. The standard maximum height was 269 ± 23 cm ($n = 42$).

Over the period January to June mortality averaged $.07 \pm .03$, and the highest rates were in February and June. Only four deaths occurred among the 34 shoots appearing while the grove was monitored, too few to obtain meaningful age-specific mortality. However, among the mixed-age shoots marked in December, survivorship was linear through the observation period (Fig. 2, B), with a loss of .06 per month ($r^2 = .99$, $s_b = .003$). The entire mixed-age cohort would thus have been lost within 17 months.

DISCUSSION

Emergence rates in all species averaged less than one new shoot per ten old shoots per month. In *A. giganteum*, a single maximum in this rate would characterize undisturbed conditions, with a peak in the wettest months. *A. subsericeum* may be similar, but the rates were undifferentiated through the short observation period. In contrast, each grove of *A. hanburyi* showed fluctuations throughout the year, of similar magnitude. If this was an endogenous feature, it is curious that the fluctuations were relatively synchronous between widely separated groves. The variation of emergence rates might be better resolved if not all older shoots were considered as the parent population, but only shoots of mature height.

The early pulse of emergence in Ag1 clearly related to manual thinning of that grove, and such a pulse may be expected in all the species after thinning by trampling (elephants) or herbivory (primates). Herbivory is a prominent feature in *Aframomum* only regarding the stems of aerial shoots. No evidence was found of damage to the rhizomes by vertebrates, or of habitual eating of the leaves. Several primates regularly eat the young stem of aerial shoots (SABATER-Pf, 1977, 1979; CALVERT, pers. com.): *Cercopithecus nictitans*, *Papio sphinx*, *Pan troglodytes*, and *Gorilla gorilla*. However, only *Gorilla* has a major impact, with *A. hanburyi* and *A. subsericeum* together forming the bulk of the diet in littoral southern Cameroon and Rio Muni. *A. giganteum*, however, is rarely eaten, and no primate herbivory is known on several other species of the district. *C. nictitans* feeding (on Ah1) was confined to the tips of the shoots, not resulting in the immediate death of the remainder. *Gorilla* destroys the entire leafy portion to reach the stem tissue, and frequently breaks off the shoot at ground level (CALVERT, pers. com.). Entire groves are not destroyed at once by *Gorilla*, although an individual may eat many kilograms of *Aframomum* stem in one day. Typically, a few stems are taken within arm's reach of a seated animal, and such feeding sites are separated by several meters (CALVERT, pers. com.). Certainly the growth rates recorded here suggest "recovery" from herbivory is rapid (see also BULLOCK, 1978).

The general pattern of height growth (Fig. 1) is apparent at all seasons and in all species. A lag phase of slow initial growth after emergence was not conspicuous. Comparing the heights at various ages to the standard maximum heights showed that *A. hanburyi* (Ah1) grew most rapidly,

attaining proportions of its maximum of $0.28 \pm .10$ at the age of 2 weeks, $0.65 \pm .10$ at 6 weeks, and $1.07 \pm .07$ at 18 weeks. *A. giganteum* (Ag2) attained $0.17 \pm .04$, $.43 \pm .06$ and $.75 \pm .05$ of full growth at these ages, and *A. subsericeum* cohorts grew to $0.15 \pm .04$, $.26 \pm .13$ and $.69$ of their standard by the same ages. The actual daily height growth these represent for 0-2 weeks and 2-6 weeks were roughly 5 cm per day for both *A. giganteum* and *A. hanburyi* shoots, but only 2.5 cm per day for *A. subsericeum*. During much of the early rapid growth the shoots bear no lamina, and so are largely dependent on translocation of photosynthate from other shoots.

The initial growth rates may be biased here by the relatively long intervals between censuses. Individuals in each cohort might differ by nearly four weeks in actual emergence date, and occasionally differ by more than a meter in height; I have taken the means to be indicative.

Flowering in *A. giganteum* and probably *A. subsericeum* occurs mostly during the peak of the rains. With no better resolution than monthly censuses, the peaks of shoot emergence and flowering cannot be sharply distinguished: these energetically costly activities may be nearly simultaneous. *A. hanburyi* flowered in a bimodal pattern, contrasting with its shoot emergence. The population was never entirely out of flower, but the peaks preceded the rainfall maxima, and flowers were nearly absent in the major dry season, resulting in a scarcity of mature fruit in May and June. The *Aframomum* species thus present equivalent growth forms but divergent relationships of vegetative and sexual phenology. Altogether, their flowering peaks may be largely non-coincident, so that these sunbird-pollinated plants warrant further comparison with similarly patterned *Heliconia* species, hummingbird-pollinated herbs of the Neotropics (STILES, 1978).

Climate-related but diverse phenologies were evidenced by two other species of forest disturbances, with different patterns in the relative timing of vegetative growth and reproduction. A study of 39 clones of *Megaphrynium velutinum* (*Marantaceae*) showed new leaf emergence was strongly biseasonal, coinciding with the wet seasons, but flowering was virtually restricted to the major dry season. The coincidence of growth and reproduction was seen in 18 clones of the suffrutescent *Palisota ambigua* (*Commelinaceae*), but in this case both activities were biseasonal, and lagged after the rainfall maxima.

Mortality in all species was strongly related to shoot age and indications of seasonality in mortality were probably due to the unimodal or periodic variations in shoot emergence. The shoots of all species probably have maximum longevities in the range of 1.2-1.5 years, in most cases with less than 10 % of the cohort dying each month. The notable difference in predicted longevity of *A. hanburyi* between shoots of known age and the mixed-age cohort suggests an increase in mortality slightly after the age of one year, beyond the scope of this study. Such a change might be due to the timing of growth of vegetative and flowering branches. Moreover, the exact age-dependence is not a characteristic of a genet, but

is also affected by herbivores, and the surrounding plants. Nearby shoots of the same grove are an important part of any one shoot's environment, at least in shading if not also in vascular interchanges.

Thorough integration of emergence rates, growth, reproduction and mortality will depend on accounting for the connection of individual shoots. Knowledge of *Aframomum* structural demography still lacks the critical elements of the relative timing of long, short and flowering branch growth. Moreover, it is unlikely that the numbers of each branch type (per existing mature shoot) is constant. Since vegetative and flowering shoots are certainly expensive productions, their growth is likely to have major effects on the growth and mortality of parent leafy shoots. However, demographic trends in clone autogeny are beyond the scope of this study.

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